

THE
PSYCHOLOGICAL BULLETIN

GENERAL REVIEWS AND SUMMARIES

THE FUNCTIONS OF THE CEREBRUM

BY SHEPHERD IVORY FRANZ

Government Hospital for the Insane, Washington, D. C.

For the understanding and for the proper evaluation of researches upon the nervous system, and especially of those on the cerebrum, it is necessary to have a knowledge of and to keep in mind the methods used for the collection of the facts which are recorded. The functional observations of the brain are derived from two general sources, the clinical and the experimental, which are not distinct but usually overlapping. The methods which have been used may be grouped under the following general headings: anatomy, physiology, and pathology. The anatomical studies have been conducted in a variety of ways: the myelogenetic, like those of Flechsig, by determining the development of different parts at different stages of anatomical and physiological development; the cyto- and myelo-architectonic, like those of Campbell and Brodmann, by which there is a finer differentiation of areas and which have led to certain physiological conclusions which will be considered below; and the general studies of human and comparative material. The physiological methods are experimental methods of stimulation and of extirpation, the former resting upon the assumption that the results of stimulation are similar or comparable to the normal working of the part, and the latter method resting on the assumption that if a part be destroyed there will be an absence of function corresponding to the normal function of that part. The general pathological methods are both anatomical and physiological; the former consisting largely of the examination of lesions and of degenerations from lesions, and the physiological, corresponding to the physiological methods of extirpation in animals, but, of course, dealing largely with human material.

With the exception of physiological extirpation all these methods have been used for the determination of function on the brain of man, but the greatest amount of knowledge of human cerebral functions has been derived from a combination of functional observations (clinical studies) and the anatomo-pathological observations of the brain after death.

The studies on man have certain advantages over similar studies on animals. The greatest advantage is the possibility of acquiring knowledge through the medium of speech of the effects of certain lesions and of stimulation, while the results from animals must be interpreted from less direct indications. On the other hand, it must not be supposed that all, and it must be admitted that very few, of the clinical studies have been the results of careful observations in a psychological sense. The possibility of careful psychological descriptions of the mental state accompanying cerebral lesions has seldom been realized, and it is the habit to record generalized deductions rather than minute observations on the mental side. Opposed to the possible advantages of the studies on man there is a decided disadvantage that we have always to deal with lesions which are naturally made and which most often extend to such dimensions that observations of small parts of the brain can not be made. The work on animals has this advantage; viz., that the lesions may be small and well defined but there is the disadvantage that the mental states of animals may differ largely from those of man.¹

Although often the diversified methods have led to conflicting conclusions it is of interest to note that von Monakow (18, 19) largely from clinico-pathological studies, Bolton (3, 4) from histological and pathological investigations and Franz (9) from experimental work have recently brought forward somewhat similar hypotheses to explain the working of the brain in the complex mental processes. Each of these investigators show differences in standpoint, but all agree that the cerebral processes are much more complicated than has hitherto been supposed. We shall take up the hypothesis of von Monakow as the representative of these three and consider it briefly. Von Monakow believes that mental disturbances are produced by brain disturbances of a very varied character anatomically, but physiologically of the type of breaks or lowered conductivity of

¹ In a review of this character it is obviously impossible to consider all the articles, books, etc., dealing with the subject. The *PSYCHOLOGICAL INDEX* for 1909 contains about 90 titles upon the functions of the brain (including aphasia) and the bibliography contained therein is not complete. Although no accurate count has been made, the writer estimates that the total number of titles, including clinical articles, on this topic would not fall short of 200 each year.

the nerve elements which are active in the production of the mental phenomena. The partial or total lack of continuity of connection is called *diaschesis*. Diaschesis is an inhibition, "eine shockartige Funktionshemmung in primär nicht lädierten, vom Herd fern liegenden aber mit diesem anatomisch verbundenen Hirnstellen." According to this conception the effects of all kinds of brain lesions may be understood, for we have to look not for special centers but for connections. Very similar clinical phenomena may, therefore, be produced by anatomically distinct lesions, if the lesions be sufficiently small and definite.

In addition to the general view of cerebral conditions Bolton and Franz have considered the functions of the so-called association areas. Bolton believes that the posterior association area is concerned to a great extent with the language function, and the anterior association area with "the highest and latest evolved functions of voluntary attention and inhibition, and of selection and co-ordination of the various individually complex processes of cerebral association" (3). Although it is not expressly stated, it appears that the view of Bolton in regard to the frontal association area is similar to that of Franz, who considers the frontal area to be what may be called the efferent part of the association and the posterior association area to be the afferent part of the association.

These two authors do not apparently agree in regard to the possibility of a strict localization of sensation, of movement and of mental processes, for Bolton believes in a strict localization of an areal character. He goes even farther in this than most adherents of the localization school, and in this he is supported by those who, like himself, have investigated the structural arrangements in the cortex. Bolton is, however, not as positive regarding the functional value of the histological studies as is Brodmann, for he says: "Beyond a relatively gross subdivision of the cerebral cortex into different areas, it is unlikely that the histological method will be of assistance, as cerebral function, even when relatively low in grade, consists of associational processes which involve many related regions of the cortex."

Brodmann (5) has given the most direct statement of a sort of phrenology from the histological standpoint. He believes in a strict histological differentiation of the brain into areas, and he asserts, but does not correlate with the histological findings, a functional differentiation and correspondence. In the consideration of this matter Brodmann uses the term 'physiologische Cortex-organologie'

to sum up his position. He has written: "Unsere Feststellungen rechtfertigen nicht nur im Princip die Annahme einer örtlichen Arbeitsteilung innerhalb der Grosshirnrindenfläche, sie beweisen auch mit unumstösslicher Gewissheit das Vorhandensein einer streng zirkumskripten regionalen Lokalisation gewisser Funktionen (p. 300) . . . die spezifische histologische Differenzierung von Rindenarealen beweist unwiderlegbar deren spezifische funktionelle Differenzierung . . . die linienscharf abgegrenzten und als besondere morphologische Organe aus der Rindenfläche heraustretenden Strukturzonen lassen sich nicht anders als durch die Annahme erklären, dass in ihnen ebenso scharf umgrenzte spezifische Funktionen lokalisiert sind" (p. 304). This is a return to Gall, if not to Spurzheim. It is not likely that such assertions without physiological facts to support them will pass unchallenged, and to the writer they seem far from proven, or even probable. This view may be taken as the extreme of deducing function from structure, but it is paralleled by the finer functional conclusions of Bolton, which, however, have some facts in support of them. I refer to the functional differentiation of the cortical layers. In regard to the layers Bolton (3) asserts that the first and fourth cortical layers, consisting mostly of fibers, may be omitted from consideration, but that the three other layers have different functions: the second, or outer pyramidal layer "subserves the psychic or associations functions of the cerebrum," the third layer "subserves the reception or immediate transformation of afferent impressions, whether these arrive directly from the lower sensory neurones or indirectly through other regions of the cerebrum," and the fifth layer "subserves the lower voluntary and instinctive activities of the animal economy, and thus forms a lower level basis for the carrying on of cerebral function." Here, apparently, Bolton passes from the extreme localization view to a more general view of the brain areas, in asserting that all areas have the same general functions, and it is difficult to make these two views cohere. Whatever may be our opinion of the hypotheses and conclusions already formulated from the cyto- and myelo-architectonic studies, it can not be gainsaid that this work is of great importance for the psychologist who has leanings towards the correlation of mental states and cerebral processes, and who takes a functional attitude.

These general matters will not be settled by hypothesizing or by strictly anatomical or histological studies. We must have functional observations to add to the anatomical facts, or we must have the anatomical observations to correlate with the physiological.

On the other hand, the functional observations must be made with as great care and with as great an amount of detail as the anatomical observations or we shall fail to bring about a correlation. One of the best examples of this is to be found in the studies of the relation of parts of the brain to speech functions. For a long time it satisfied most people to believe that the aphasias could be divided into the motor and the sensory, or into cortical, subcortical and transcortical, but because of the work of Marie and of von Monakow much doubt has been cast upon the validity of a strict anatomical localization and upon the discreteness of the supposedly different types of aphasia. We may pass over the matter which has caused much useless discussion, viz., the relation of aphasia to dementia or to mental deterioration, because that is to be settled only by definition, for the most important matter in connection with the discussion of speech and its disturbances is the consideration of the discreteness or the individuality of separate elements in speech. Physiologically, the understanding of vocal sounds, of gestures, of writing, etc., and the emission of movements expressive of bodily feelings and of ideas are to be understood only by taking the view that these are processes of association, and the disturbances of the ability to make movements expressive of ideas, or disturbances of the ability to understand are due to defects or faults in the association ability (physiologically considered) of the brain. The old doctrine dies hard, however, and there are many who still believe in a rather strict localization of visual images of words, auditory images of tones, kinesthetic images of vocal cord, tongue, etc., movements, which are supposed to be absent in certain aphasic conditions. (See 1, 2, 10, 11, 14, 15, 20.)

Although apraxia is an aphasic condition, often resulting from or coincident with lesions of the association fibers of the corpus callosum, and has been studied most by Liepmann, this author disregards the association explanation of Marie, and tends toward a view similar to the old classical localization (15). Beduschi (2) also cites cases apparently opposed to Marie's view, but with slight modifications in explanation all the cases may be brought into the category of association disturbances, and here the diaschisis hypothesis of von Monakow is most enlightening (17, 18).

Of association disturbances other than those connected with speech, it will be recalled that Franz, in 1902, found a loss of habits following the extirpation of the frontal lobes. This result has now been confirmed by the work of Kalischer (12), who has found losses of auditory-motor associations following the destruction of the frontal

areas. He has furthermore confirmed the earlier results in as far as the effects of the removal of one frontal are concerned, for he has also found that the removal of one frontal produces a disturbance of the association, but not an actual loss. In these experiments, however, the dogs which he used did not show an ability to relearn the habits which were lost after the removal of the frontals. From his work the conclusion is drawn that the frontal lobes are inhibition centers, because after the removal of the frontals the animals did not inhibit movements which they had been taught to inhibit. With equal value it might be said that the untrained dog, which retains its frontal lobes and does not inhibit instinctive actions, has no inhibition function. These results (of Franz and Kalischer) are the only ones which indicate clearly an association function for the frontal lobes in animals, and they are the only ones which indicate an association function for the brain of animals or man other than those connected with speech.

The histological differentiation of the brain into areas different from those into which the fissures divide it has led to newer work on the physiological differentiation and definition. The researches of Sherrington and Grünbaum antedated the histological differentiations, but resulted in a physiological differentiation of the motor area different from that which had previously been believed in. These authors placed the motor cortex anterior to the fissure of Rolando, and their results have been amply confirmed by the Vogts, by Lewandowsky and Simons (16), by Cushing and others. The extirpation of the precentral cortex is followed by paresis in animals, and the extirpation of the precentral cortex leaves the post-central cortex unstimulable (Lewandowsky and Simons). These results show that the cortex posterior to the Rolandic fissure has no fibers going directly to the muscles and that the movements which sometimes result from stimulation of this area are caused by the transfer of the stimulation or the association conduction of the stimulation to the neighboring motor region.

The article by Cushing (8) on the stimulation of the cortex in conscious patients is one of the most noteworthy contributions to the understanding of the brain which have appeared in recent years. It is not often that the brain in man is exposed so that during conscious waking states the results of manipulation and stimulation can be determined. Several cases of a character requiring surgical intervention, but in which it appeared inadvisable to use the ordinary methods of general anesthesia, submitted to the examination by

electrical methods of certain areas of the brain, and Cushing was able to demonstrate beyond doubt that the post-central convolutions are concerned with sensations from the skin and the underlying tissues.

Other sensory areas have not been investigated in such a manner in the brain of man, and for our information regarding the location and the extensivity of these areas, we must depend upon the correlation of sensory defects (of vision, hearing, etc.) with the post mortem findings, and upon animal experimentation. The methods of training, first extensively used by Franz for the determination of the association functions, has been utilized by Kalischer, by Swift and by others for the determination of the extent of certain of the sensory areas of the cerebrum in animals and it appears to be settled that the temporal lobes are concerned with the perception—not only sensation—of sound. Swift (21) has shown that, corresponding with the results obtained by Franz in connection with the frontal lobes, after an animal has lost auditory-motor habits following the destruction of the temporal lobes it may relearn similar habits. The details of this work have not appeared and it is difficult to make a close comparison with the similar work of Kalischer of a few years ago. It appears, however, that the former work of Kalischer and the later work of Swift are in agreement. Kalischer (13) has, furthermore, investigated the functions of the occipital lobes by the training method, and his results are in accord with certain clinical observations, and with previous physiological experiments. Since this matter will be taken up for full consideration by the writer at an early date no further mention of it will be made here.

There remains space only for the consideration of the work of Graham Brown (6, 7), who has studied the effects of the removal of parts of the cortex on certain reflex functions. It has been shown that after a part of the cerebral cortex is removed the reflexes on the ipsilateral and those on the contralateral sides differ. The flexion excitability is increased upon the same side and the extension excitability is increased upon the crossed side, the scratch reflex may be abolished on the crossed side or the excitability of the reflex may be greatly lowered, while on the ipsilateral side there may be little change. These results indicate the extent of cortical control over functions which are often, but incorrectly, believed to be absolutely independent of the higher centers, and the work is to be considered in conjunction with that of certain Italian investigators, who found the reflex time to be increased upon stimulation of the frontal area.

Finally it may be said that the recent work on the histological differentiation of cerebral areas is most important for a definite understanding of functional localization, but it does not appear, either from the experimental or the clinical investigations, that the brain is a simple organ with simple but numerous functions, nor does it appear that efforts to bring about a revival of the doctrine of Spurzheim, even though it be based upon these anatomical studies, will help materially to advance the knowledge of this 'vehicle of mind.'

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THE COÖRDINATIVE MECHANISMS OF THE CENTRAL NERVOUS SYSTEM

BY ROSWELL P. ANGIER

Yale University

It has seemed worth while, in this first physiological number of THE BULLETIN, to present some of the leading results of one of the most illuminating books¹ on the functions of the nervous system that have appeared in years, although it is now nearly six years old; the more so because it has had no full review in the REVIEW publications and only scanty notice in most other journals. Nor is there much evidence that its results have sifted into general psychological literature. This may be due in part to Sherrington's condensed and difficult exposition. I shall attempt no full review but shall simply emphasize certain vital points concerned in nervous coördination, or integration. Curtailed space prevents my discussion of the later results of Sherrington and others, many of which will be found, however, in Woodworth's article in this number.

The unit mechanism in nervous coördination is the reflex arc. Two clear fields of investigation therefore open out: (I.) the coördinating activity of the simple arc, and (II.) the type of coördination effected by the compounding of such arcs.

I. *Coördination in the Simple Arc.*—The main function of the receptor is "to lower the threshold of excitability of the arc for one kind of stimulus, and to heighten it for all others" (p. 12). Its chief contribution to reflex mechanism is, therefore, *selective excitability*, by which, to a degree, confusion among reactions is forestalled.

The contributions of the reflex-arc to nervous integration rest, however, chiefly on the properties of nervous conduction in the arc as distinguished from those in nerve-trunk. The full list may be found on p. 14. Conduction in reflex-arcs exhibits, among the others, these eight characteristics: (1) "slower speed as measured by the latent

¹SHERRINGTON, C. S. *The Integrative Action of the Nervous System*. New York: Scribner, 1906. Pp. xvi + 411.

period between application of stimulus and appearance of end-effect, this difference being greater for weak stimuli than for strong." In nerve-trunk any delay is due wholly to propagation time, nor is there good evidence that the speed of conduction is less with strong stimuli than with weak. This *identity* of speed in nerve-trunk from strong and weak stimuli alike and the great *difference* in speed in reflex-arc from strong or weak stimuli respectively is important (*e. g.*, it strengthens the argument that the delay is due to some structure other than nerve fiber proper; it enables an organism to respond with varying degrees of rapidity to stimuli of varying degrees of intensity). Sherrington then discusses the question whether the latent time is consumed in 'setting' or establishing a connection between neurones in an arc, the current thenceforth flowing perhaps as fast as in nerve-trunk, or whether it is inherent in the process of arc-transmission. He inclines towards the latter position, since if a flexion reflex of the hind limb of a spinal dog be elicited and then, while flexion is still in progress, a stronger stimulus be suddenly introduced, *there occurs only a negligible reduction of the latent time for this incremental reflex from that of the initial reflex*. It appears, therefore, that the latent time is due to a process the same in nature, whether in initiating a reflex from a resting arc, in increasing a reflex already in submiximal activity, or, probably, in maintaining a reflex in unaltered continuance. These considerations argue against any supposition of amœboid movements as controllers of conduction between neurones and, since even while at rest the arc is as well prepared for immediate transmission of impulses as when actually engaged in activity in the very direction the new impulses would require, they argue a greater need for active inhibition in the coördination of arcs that employ a final common path but for different purposes. (2) "Less close correspondence between the moment of cessation of stimulus and the moment of cessation of end-effect, *i. e.*, there is a marked 'after-discharge.'" The phenomena of latent period and of after-discharge enable us to characterize conduction in arcs as exhibiting inertia and momentum. After-discharge is an analogue to the visual positive after-image. (3) "Less close correspondence between rhythm of stimulus and rhythm of end-effect." Sherrington's work on this well known principle shows that (as is also true for the latent period) different reflexes have different rhythms developed, doubtless, to meet the peculiar adaptive purpose of the given reflex. (4) "Less close correspondence between the grading of intensity of the stimulus and the grading of intensity of the end-effect." Such grading is,

however, found in arcs. The 'all-or-nothing' principle does not there hold. The increase in the reflex effect is in power and in amplitude; the rhythm changes little. This adaptability of power and amplitude, like that of speed, to intensity of stimulus, is manifestly biologically valuable in many reflexes. As to the problem whether the increase in response to graded stimuli is due to more muscle fibers being involved or to a greater intensity of nervous impulse in those already active, Sherrington leans to the latter alternative, because the mechanism of a reflex is, although anatomically a collection of units, itself a unit, and discharges as a unit. Even the phenomenon of nervous irradiation supports this view, since the irradiative progress to new muscle is sudden—a progress from unit center to unit center. (5) "Considerable resistance to passage of a single nerve-impulse, but a resistance easily forced by a succession of impulses (temporal summation)." (6) "Irreversibility of direction instead of reversibility as in nerve-trunks." (7) "Fatigability in contrast with the comparative unfatigability of nerve-trunks." (8) "Refractory period, 'bahnung,' inhibition, and shock, in degrees unknown for nerve-trunks." *Refractory Period:* The phenomenon of rhythm in nerve-cell discharge is itself presumptive evidence of a refractory phase. In reactions of the central nervous system it is "a state during which, apart from fatigue, the mechanism shows less than its full excitability" (p. 45). In the scratch-reflex, for instance, flexion and extension each occurs at a rhythm of from 4 to 6 per second. This rhythm is *independent of the rate of stimulation and remains unaltered under increased intensity of stimulation*. It appears, therefore, that when after each contraction of the flexor concerned in scratching the extensor phase of the reflex supervenes, no intensity of stimulation can excite the now inhibited or refractory flexors to activity, and the same may be said of the extensors when the flexors are active. The flexors and the extensors exhibit, that is, a rhythmic alternate 'refractory phase.' It is apparent that in cyclic actions occurring in rhythmic series (scratching, swallowing, blinking, rhythmic stepping of the limbs, etc.) the phenomenon of refractory phase contributes immensely to the coördinated result.

Even from this enumeration of the characteristic differences between nerve-trunk and reflex-arc conduction it is evident that many of the constant as well as the variable *integrative* features of the 'simple' arc are determined by its own conductive peculiarities. Different reflexes, too, to an enormously greater extent than do different nerve-trunks, exhibit, *inter se*, differing peculiarities of con-

duction (*e. g.*, different latent periods, rhythms, refractory periods, and varying degrees of grading of response to graded stimuli); their individual *conductive* idiosyncrasies obviously determine, in part, at least, their individual *coördinative* or *integrative* differences developed in biological adaptation.

As to the physiological loci of most or all of the foregoing differentiae of reflex-arc conduction, the synaptic surfaces of separation between neurones, in the gray matter, appear the most probable, especially since less and less influence on conduction is being attributed to the nerve-cell body. As an example of the type of Sherrington's reasoning, in seeking the locus of the phenomena observed, let the following, concerning the refractory phase, suffice. The 'scratch-reflex' is elicited by stimulating any point or points within a large saddle-shaped field of skin on the back and sides of the spinal dog. The mechanism of this reflex consists probably of an afferent neurone (or a bundle of them), a long descending proprio-spinal neurone (determined by tracing the course of degeneration), and a motor neurone. At least two synapses are, therefore, involved. Now the seat of the refractory phase can be neither in the motor neurone (or final common path) nor in the end plates in the muscle, since, when excited directly or through nerve-trunk, muscle exhibits no refractory phase nor, furthermore, is it present when the motor neurone is used by other reflexes (the flexion reflex) or excited to contraction through the pyramidal neurones from the cortex. It does not lie in the skin nor in the afferent neurones, since, when the reflex is in progress from an excited point *A*, the excitation of another point *B*, within the stimulus area, does not alter its rhythm nor complicate it in any way. This fact points to a part of the reflex mechanism common to impulses from both *A* and *B*. This cannot be, however, any nexus between the afferents, since we have no knowledge of a collateral connection between afferent neurones. The refractory phase may be referred, therefore, with great probability, to the synaptic connections between the proprio-spinal neurone mentioned and the afferent paths *A* and *B*, through collaterals from their ascending-descending branches. It must at least be *central* to the afferent neurone and the motor neurone concerned.

II. *Coördination between Simple Reflexes—the Compounding of Reflexes.*—A natural transition to the consideration of complexer reflex-patterns lies through the phenomena of 'inhibition.' The refractory phase in the single arc is itself a form of inhibition. If, further, the flexion-reflex be evoked in the hind leg of the spinal dog

by stimulating, say, the foot, it is found even by direct palpation, that the knee extensors of the same knee are actively inhibited, even as to their tonus; complete relaxation ensues. This is typical of any opposed muscle groups at the same joint, inhibition in one group of muscles being the *simultaneous* counterpart to excitation in the opposite group. Any such flexion involves, therefore, two simultaneously acting reflexes—perhaps the simplest type of coördination between simple arcs. The *same afferent impulse* utilizes two opposed arcs to opposite effect. The seat of the duplex process is intra-spinal and doubtless synaptic. Nor can any mere increase in intensity convert the inhibitory effect into an excitatory; further, when one reflex is employing given muscles, other reflexes are normally inhibited from utilizing them. These two facts clearly show that the great biological contribution of inhibition to the organism is to fortify momentarily dominating reflexes in the possession of their arcs until some shift in the environmental constellation of stimuli brings to orderly prepotence further adaptive reflex acts.

Inhibition is thus one of the chief mechanisms of integration. Another is 'alliance.' Properly to understand them it is, however, first necessary to refer to what Sherrington calls the principle of the *final common path*. The various receptive neurones are so many private paths, each sacred to its own adequate stimulus. Any given private receptive path may, however, eventually play on a great number of different effector organs and, conversely, many such private paths may converge on one effector. The motor neurone leading to the effector, becomes thus a 'final common path,' a public path, receiving impulses from many afferent arcs, each using it, perhaps, to slightly different purpose. Certain consequences of this principle are (1) the essential qualitative identity between impulses arising in different afferent nerves, (2) the capacity of the final common path to respond to all the different rhythms of the different reflexes employing it—its aperiodicity, and (3) the necessity of successive and not simultaneous use of this path. Nervous coördination reduces largely, therefore, to a competition among various reflex arcs for the possession of the final common path. Inhibition is one of the determinants of the outcome. Another is 'reflex alliance.'

'Alliance' means that various reflex arcs reinforce one another's action on one or more final common paths. If points *A* and *B*, as much as 10 cm. apart, in the receptive area of the scratch reflex, be stimulated, each subliminally, the reflex occurs. If the stimuli are

supraliminal it will be increased. This is not primarily due to the excitation of different groups of fibers in the final common path,¹ but to the *intensive augmentation of the same fibers*, since the scratch, initiated by *A*, does not alter in rhythm when *B* alternates with *A*. Impulses from all points of the receptive field embouch, therefore, on the *same* final common fibers: the mechanism is a unit, composed of many allied reflexes. A more extensive type of alliance is seen in the mutual reinforcement between extero-ceptive (external stimuli) and proprio-ceptive (internal stimuli, *e. g.*, kinæsthetic) sensitive fields, typified by many reflexes, involving, first, a response to an external stimulus, second, the consequent excitation of sensory organs in the contracting muscles and, third, an alliance between the two sets of arcs, both acting on the same final common path. There are, however, still wider alliances than these, namely, those involving arcs from widely scattered sensory points. If, for instance, the various digits of the hind foot of a bulbo-spinal dog are stimulated, they mutually reinforce one another's action on the final common path of the flexion reflex: to these there may ally themselves impulses from the crossed fore foot, the tail, the crossed pinna, and, doubtless, in the intact animal, from the otic labyrinth, the olfactory organs and the eyes. Furthermore, just as reflexes may be allied in exciting a muscle they may be allied in inhibiting it. And the inhibitory alliances may be either simultaneous or successive. Whenever, for instance, a simultaneous alliance is in progress, *an inhibitory alliance of all the arcs to the contrary muscle groups, relaxing them, is involved*; whenever one group of reflexes dispossesses another from the use of the final common path we have successive inhibition or 'interference' and, finally, when "the threshold of each succeeding reflex is lowered by the excitation just preceding its own" (p. 184), we have successive alliance. A given reflex usually lowers the threshold for succeeding allied arcs but it may also lower it for antagonistic arcs: in the stepping reflex of the dog—and this is doubtless typical of most 'alternating' reflexes—an antecedent reflex not only brings about an ensuing stimulus for the opposite movement, but predisposes the opposite centers to activity. Such alliance between mutually inhibitory successive reflexes obviously favors the orderly prepotence of the successive units of a biologically valuable serial act. This coördinative interplay of successive reflexes is nicely seen, too, in the so-called 'compensatory reflex'—"a return to a state of reflex equilibrium which had been disturbed by an intercurrent reflex to which the compensatory reflex is the diametrical antagonist"

¹See above, differences between reflex-arc and nerve-trunk conduction, (4).

(p. 203). In the state of 'decerebrate rigidity' of the muscles the flexion reflex breaks in on a strong reflex tonus (active extension) and the reflex itself induces supervening tonus, stronger, often, than before, probably largely through the afferent nerves of joints, muscles, etc. These proprio-ceptive nerves, together with those of the otic labyrinth are, indeed, probably responsible for the tonus of the skeletal muscles—itsself a reflex and involving always coincident tonal inhibition of muscles antagonistic to those in tonus.

One important matter remains. Manifestly the orderly sequence of *reactions* in an organism is not determined by any orderly sequence of *stimuli*. The organism is, rather, always exposed to a jumbled constellation of stimuli, shifting from moment to moment, some of which secure at any instant prepotence over the rest, to be then displaced by others. What factors determine, chiefly, the order of prepotence among the arcs competing for possession of the final common path? One is *spinal induction*; a given stimulus, by central spread, lowers the threshold for allied arcs and, as we have seen, for the arcs next to supervene, *e. g.*, in 'alternating' and in 'compensatory' reflexes. Secondly, *fatigue* loosens the hold of a reflex on the final common path, assisting, thus, to serial variety of reflexes; for the final common path is itself relatively indefatigable—the seat of the fatigue being, doubtless, intraspinal. Third, the *intensity* of reaction of the afferent part of an arc, relatively to its rivals, is perhaps the most powerful influence determining prepotence. Both intensity of stimulus and degree of excitability of the afferent arc are, of course, here concerned. Fourth, the *functional species* of a reflex contributes to determine prepotence. In the cord noci-receptive reflexes—those usually elicited by harmful stimuli, or stimuli arousing pain in an intact organism—tend to displace other reflexes. Examples are the flexion-reflex (injury to foot) and the scratch-reflex (bite of flea). Further, however, any reflexes evoking strong affective accompaniments in the intact animal, are likely to be prepotent, *i. e.*, the sexual. These types of reflexes stand, thus, at the upper end of the prepotency scale—the most difficult to dispossess—while at the lower end are the tonus reflexes that maintain habitual attitudes and postures. Finally, all four of these factors determining reflex prepotence are reducible to intensity of reaction.

REFLEX ACTION

BY R. S. WOODWORTH

Columbia University

The past two years have witnessed several interesting developments in the knowledge of reflex action. Sherrington's 'decapitate preparation' (9, 6) affords a convenient means of studying and demonstrating the functions of the mammalian cord. After ligaturing the carotid and vertebral arteries, and, indeed, the whole neck with the exception of the trachea, he simply beheads the animal; after which the anesthetic can be dispensed with, and the animal kept alive for several hours by artificial respiration combined with sufficient warmth. On such a preparation, Sherrington (8) has examined the theoretically important scratch reflex in the cat, and finds that the rhythm of the scratching movements originates in the cord and not in the sense organs, since it appears on exciting the cord itself.

What may be called 'switching reflexes' are brought to light by the observations of Magnus (3). The reflex movement elicited from the leg of a spinal dog differs according to the posture of the leg. The same stimulus which gives flexion from a position of extension gives extension if the limb is already flexed; and it is possible for the experimenter to switch the movement back and forth from extension to flexion by simply altering the initial position of the limb. These effects are not obtained if all of the sensory fibers of the limb are severed by section of the dorsal roots, but they are not destroyed by injections of cocaine, stovaine, etc., beneath the skin or into the joint capsules. The afferent fibers concerned are therefore those from the muscles; the 'switching' is a function of the proprioceptive system. Afferent impulses from the muscles so set the switches in the cord as to determine the reflex path of other impulses.

Similar instances of switching are shown by Magnus (4) in case of the scratch reflex. When a spinal dog is standing, irritation of the skin causes the leg of the same side to scratch, while the leg of the opposite side is extended and abducted as if to support the body. If, however, the animal is laid on its back, the scratching may be bilateral; but either leg can be prevented from participating in the rhythmic movement by holding it gently in a position of extension and abduction. This also is a proprioceptive effect. But similar effects can also be produced by cutaneous or subcutaneous stimuli; for if the animal is laid on one side, or if one side is pressed against, it is always the opposite leg that scratches, on whichever side the

stimulus to scratching is applied. Thus both pressure on one flank and extension and abduction of one leg tend to switch the scratching movement to the opposite leg; if these two influences act counter to each other, pressure on the flank yields to the posture of the limb, and the latter influence controls. We get here some insight into the complicated spinal mechanism governing the selection of reflexes.

Further examples of proprioceptive reflexes are brought out in Sherrington's recent work (7). In certain conditions (decerebrate rigidity especially, but also in spinal preparations), when a muscle which is in tonic contraction is forcibly stretched, it yields to the stretching force, gives up part of its contraction, and assumes a new length or degree of contraction, maintaining this after the stretching force has ceased to operate. This is the 'lengthening reaction'; and an opposed 'shortening reaction' can be induced, in the same conditions, by shortening the muscle. The muscle is plastic; it retains, by its own contraction, the length which has been impressed on it. This it no longer does if its afferent nerves are severed, though it needs no other afferent nerves than its own. Not only its tonus in general, but the plasticity of its tonus, is dependent on a reflex arc starting in its own sense organs, and leading through the cord back to itself. These strictly local reflexes are probably important in adding duration and steadiness to movements induced by other stimuli, in maintaining postures, and in modifying reflex and perhaps voluntary movements in accordance with the resistance encountered.

The relations of several important reflexes—the flexion of a limb and the extension of the opposite limb, the stepping reflex, and standing and walking—are subjected to minute analysis by Sherrington (10). The simple flexion reflex, by which the leg is withdrawn from a noxious stimulus, involves the contraction of certain muscles and the relaxation of others; and the same muscles are involved whatever be the intensity of the movement. Increasing the force of the response does not mean the bringing into play of new muscles, but a more complete excitation or inhibition of the same muscles. The reflex may however spread to the opposite leg, inducing there, usually, an extension. The 'stepping reflex' of the spinal animal comprises alternate flexion and extension of the hind limbs; and the flexion is almost identical with the simple flexion reflex, and the extension with the extension reflex. The main peculiarity of the stepping reflex is its rhythmically alternating character. It consists in an alternation of antagonistic reflexes, though it may be aroused

and maintained by a continuous stimulus. Several factors probably combine to produce the alternation: a proprioceptive reflex from each muscle excited, leading to the inhibition of that muscle and the excitation of antagonists; a 'switching' of the original stimulus, such as was noted by Magnus; and a purely central rebound effect, by which the spinal mechanisms inhibited in each phase of the stepping tend of themselves to become active the next instant. *Standing* is only imperfectly executed in a purely spinal animal, but becomes fairly efficient when the midbrain and everything below is left intact. It consists essentially in a tonic excitation of extensor muscles, with inhibition of the flexors; and this reflex is of the proprioceptive order, depending, for each extensor muscle, on afferents from that same muscle. The plastic nature of this extensor tonus permits the standing posture to vary according to the conditions. *Walking*, which also occurs in decerebrate animals, is a combination of the standing and the stepping reflexes; the stepping does not altogether inhibit the composite extensor tonus, but alternately weakens and reinforces it in different muscles and in due sequence.

Brooks (1) contributes to the study of the perplexing problem of 'spinal shock,' first by introducing quantitative methods (measurement of the stimulus needed to arouse a reflex), by which means he is able to demonstrate minor degrees of shock in animals which do not show the phenomenon to ordinary observation; and second, by showing the existence of shock after cutting the dorsal roots as well as after transection of the cord. He also finds that those species which show severe shock after spinal transection show it also after cutting the dorsal roots, whereas those which show little loss of reflex excitability after the former operation show little also after the latter. The results favor the interpretation of shock as a loss of spinal tone due to the cutting off of normal excitants, rather than as a stoppage of reflexes due to injury of the paths directly involved.

Porter (5) applies quantitative methods in the endeavor to penetrate the secret workings of the vasomotor center. He argues that, if the bulbar cells take an active and directive part in vasomotor reflexes, their influence should be visible in distorting the statistical distribution of the reflex effects; whereas the variation of the reflex blood pressure, under uniform conditions, shows a 'normal' or symmetrical distribution, free from any sign of a distorting influence. Moreover, the curve of relation between intensity of stimulus and energy of response shows the same form as in direct excitation of a muscle. He thinks it probable, accordingly, that the bulbar center

does not actively 'govern' or 'control' or 'preside over' the vasomotor system, and calls attention to the unverified assumptions underlying these figurative ways of describing the function of nerve centers.

Is the knee jerk a true reflex? Snyder (11) and Dodge (2) answer in the affirmative. The latency of the action current of the muscle, as determined by Snyder, varies from 8 to 15 σ , with an average of 11 σ , when the tendon is struck, but is much less (2.5 to 3.6 σ) when the muscle is excited by an electric shock. The delay of the jerk is thus too great to be explained as a latency of direct muscular response. On the other hand, if Piper's recent determination of the velocity of the nerve impulse (120 meters per second) be accepted, and Snyder has verified it, the time necessary for a reflex from the knee to the quadriceps may be as little as 15-18 σ , and thus not far from the observed latency of the knee jerk.

Dodge also calculates the reflex time to be in close agreement with the observed latency of the knee jerk; and in addition he adduces several other lines of evidence, among which the most striking is perhaps the fact that the contraction of the muscle does not start at the point of application of the blow, but, if anything, at the opposite or proximal extreme of the muscle. Dodge's work contains a critical study of the technique of registering the knee jerk. He adopts a record of the thickening of the muscle, by mechanical or, even better, by photic transmission, as the form of record most free from errors. He examines the dependence of the latency and force of reaction on the force of the blow; and, by stimulating with a rapid series of blows, he finds the knee jerk to have a refractory period of about one tenth second. Many other results of his valuable study must here be passed by for lack of space.

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THE PRESENT STATUS OF THE NEURONE THEORY

BY H. B. FERRIS

Yale University Medical School

There are four main theories of the development of the nervous system which are held with certain modifications by the various investigators.

They may be enumerated as follows: (1) The von Baer-Hensen or intercellular bridge theory, which is defended in a modified form by Hans Held. (2) The Schwann-Balfour or cell chain theory. (3) Hertwig's theory. (4) The His-Cajal-Waldeyer or the neuroblastic outgrowth theory.

The von Baer-Hensen theory may be briefly stated as follows: that as a result of incomplete cell division the various cells are connected by protoplasmic bridges, and by a process of local differentiation in the cells and their protoplasmic connections, the nerves are formed.

This has been modified by Held (4) who accepts as true the protoplasmic connections or plasmodesms, but claims that the nerves are formed not by local differentiations but by the outgrowth of neurofibrils from the neuroblasts.

These fibrils follow the preformed protoplasmic pathway which not only guides them to their end organs but assists, Held assumes, in some unexplained way in the process of differentiation.

The Schwann-Balfour or cell chain theory essentially assumes that a nerve is developed by a series of cells joined end to end which thus forms a path from the central nervous system to the end organ. At present the most notable exponents of this theory are O. Schultze and Bethe, the latter holding the theory in a modified form. The cells of Schwann of the neurilemma are the cells which are supposed, by end to end junction, to form the nerve. These have migrated chiefly from the ganglia along the dorsal roots or, in some cases, partly from the wall of the neural canal along the ventral roots. Harrison's experiments however on the developing nerves of the tadpole have shown that even when no cells of Schwann were present the nerve

fibers developed as usual. Also his observations on the growth of the axones of tadpole neuroblasts in frog lymph, and similar observations by Burrows in the case of the chick (which will be referred to later) make it impossible longer to hold this theory. Held has also called attention to the fact that the lack of nuclei in the region of the outgrowing axone militates against the cell chain theory.

Hertwig's theory, like Hensen's, assumes that the cells of the central nervous system are connected with the peripheral end organs by the intercellular protoplasmic connections, but while Hensen considers this a primary connection, the Hertwigs look upon it as a secondary one.

The fourth or the His-Cajal-Waldeyer theory is the one more generally held, having among many others as supporters, Retzius, Lenhossék and Harrison. This theory was originated by Kupfer but especially developed by His. It essentially holds that nerve fibers and dendrites are outgrowths of certain embryonic neural cells, the neuroblasts, which by growing to the periphery, connect the end organ with the nerve centers: that these cells or neurones constitute genetic, nutritive and functional units, and that their processes lie closely applied, but never or perhaps rarely are fused as a secondary concrescence.

Gerlach's nerve network in the gray matter between the cells is not a network of anastomosing fibrils, but rather a plexus of inter-twisted fibrils. The outgrowing axones pass through the intercellular spaces, and not through the protoplasmic cell connections as is postulated by the Hensen-Held theory.

In a consideration of the neurone theory it is essential that we have clearly in mind what we mean by that term, as often considerable confusion has arisen in the discussion of the theory on account of the different interpretations and use of the term, resulting in needless conflicts and retarding the search for truth.

The essential fact of the neurone theory is that a nerve cell, and its processes, axones and dendrites, are developed from a single formative center, the neuroblast. These may be primarily or secondarily connected together by protoplasmic processes forming a syncytium but the perinuclear protoplasm constitutes a formative center and the nucleus controls the synthetic metabolism. The neurone is in a certain way, therefore, the functional as well as the structural unit. If the cell body and nucleus are the genetic and formative centers, it matters not if some of the processes may primarily be united as a result of a partial cell division, or secondarily form by

fusion with other cells, a syncytium. The cell evidently is not always the discrete unit we formerly considered it.

The evidence in regard to the genesis and minute structure of the nervous system is derived from the following sources:—histology, embryology, experimental pathology and experimental embryology.

The increase in our knowledge of the histology of the nervous system has been largely dependent upon improvements in the microscope; and in devising new micro-chemical methods which will show finer structural differentiations. So we find that the invention of the chrom-silver methods as used by Golgi and Cajal, the methylene blue and gold chloride methods, and finally the more recent technique of staining neurofibrils, have constantly advanced our knowledge of the nerve cells and their relations.

The difficulty here is that we are dealing with such minute objects, and so closely related, that it is almost impossible to tell, for instance, whether fine fibers are fused or only lie closely applied; so that it is possible for skilled observers to interpret the same appearances very differently. Also, micro-chemical methods sometimes stain partially, or imperfectly, failing to show at all times fine details completely. These various reasons partly explain the diversity of opinion, especially in regard to details of structure.

Recent histological work has added but little to our knowledge of the nervous system, but one of the most noteworthy contributions is the work of Hans Held (4). Here he not only explains his own investigations, but considers critically the bearing of various other investigations on our knowledge of the genesis and finer structure of the nervous system. Held discusses the process of neurofibrillation, the development of the motor and sensory nerves and of the sympathetic system, the histogenesis of nerve and glia cells, and the nature of nerve formation. He studied material from various animals representing the different classes of vertebrates including the Leptocardia and Cyclostomata. Briefly considered he finds that the process of neurofibrillation is much the same in the various classes of vertebrates, starting near the nucleus and on one side, in the fibrillogenous zone, forming a net-work and extending out into the plasmodesms. In the motor nerves the process starts in the neuroblasts in the neural wall, and extends through the intercellular bridges to the myotomes, and in the sensory spinal nerve neurofibrillation begins in the cells of the dorsal ganglia which have previously migrated from the neural crest.

In certain sensory cranial nerves neurofibrillation begins both

in the ganglia and in the groups of ectoderm cells of the branchial region. In both spinal and cranial nerves and in all classes of vertebrates the neurofibrils extend from the neuroblasts through the protoplasmic bridges to the end organs. That the neurofibrils may grow through the cells of the neural wall, as Held claims, seems evident from his plates. This has also been described by Harrison (3). Held's figures seem to uphold his assumption that the neurofibrils also grow through the mesodermal plasmodemes. The probability is that the outgrowing axones pursue a fairly direct course to their end organs, passing through both the intercellular spaces and cells also, if they are in the way. Whether the guiding force is of the nature of chemotaxis or some other tropism is not known.

Held assumes that if the neurofibrils grow out from a neuroblast and pass through the protoplasmic intercellular connections, this negatives the neurone theory. According to our understanding of the neurone theory this is not the case. So long as the process grows, or neurofibrillation extends as a result of the formative energy of the nucleus and perinuclear protoplasm of the neuroblast, it makes little difference where the outgrowing process goes, whether through intercellular spaces or cell protoplasmic connections.

Held's assumption that the protoplasmic processes in some unexplained way are necessary for the growth of the axone and the neurofibrillar differentiation is, we believe, not well grounded. If it be true that the neurofibrils in the cell bodies of two neuroblasts fuse together and extend out into processes as Held has described in his poly-neuroblastic formation, this would constitute a serious menace to the neurone theory. It seems to the writer, however, that the evidence for this is not satisfactory, and that Held's findings from his study of neurofibrillation and the histogenesis of the nervous system in the various vertebrates are not such as to negative the neurone theory.

Kato (5) agrees with Held that the neurofibrils form a network in the cell, especially about the nucleus. Even fibrils in the processes divide and unite with one another. Whether such networks exist or the fibrils are free and separate in the cells and processes, is of no importance so far as the truth of the neurone theory is concerned. Van de Velde (9) has described the terminal neurofibrils as penetrating the cells of Grandry's corpuscles. This is contrary to the work and the general opinion of most anatomists, which is to the effect that nerves terminate peripherally in fine fibrils on the epithelial cells, but do not penetrate them. So far as the truth of the neurone theory

is concerned, however, it matters not whether the peripheral nerve terminations are intra- or extra-epithelial.

It seems probable that we have nearly reached the limitation of the microscope and present methods in the elucidation of the finer structure of the nervous system, and can only hope for further advancement on the purely histological side, through the invention of new methods of technique. Ultramicroscopy has not yet contributed much to the elucidation of the subject (1).

On the other hand, experimental embryology has already made substantial contributions to our knowledge of the neurone, and its promise for the future seems bright.

The facts of experimental pathology bear perhaps only indirectly on the neurone theory. The evidence is, however, decidedly favorable to this theory. Waller long ago showed that the nerve degenerated when it was separated from the cell body, *i. e.*, from the nucleus, the center of synthetic metabolism. More recent investigations have shown that correlated changes also occur in the cell body, Nissl's granules undergoing chromatolysis and the nucleus shifting to the periphery, the so-called retrograde degeneration of Nissl. Likewise, changes are found in the neurofibrils as recorded by a number of observers (Sala and Cortese, 7). These changes can best be understood on the supposition that the nerve fibers are an integral part of the cells and dependent on the nucleus and perinuclear protoplasm as the formative and nutritive center. This harmonizes with the neurone theory.

In spite of Bethe's experiments on regeneration of severed nerves in dogs, in which he thought he proved that the peripheral part was regenerated by the autogenous action of Schwann's cells, the general experimental evidence is decidedly contrary to his conclusions. Most observers have described the regeneration of the nerve as an outgrowth from the central end, and this, too, would naturally be expected if the neurone theory be true. While such regeneration was supposed to hold only for peripheral nerves, it has recently been shown that regeneration may occur to a certain extent in the central nervous system (Perrero, 6). Here, too, the outgrowth occurs from the ends still attached to the cell bodies.

That the cell body or perinuclear protoplasm is the functional and nutritive center is indicated by the fact that changes occur in Nissl's granules and the neurofibrils as the result of exhaustion, starvation, the action of many poisons such as strychnine, arsenic and alcohol, also in many psychoses. The same is indicated by the observations

of Schutz (8) on the pathological changes in nerve cells, who found that fragmentation of fibrils begins in the cell bodies and proceeds peripherally, and the repair of neurofibrils also proceeds from the nucleus to the periphery.

Experimental embryology has done more to substantiate the neurone theory than any other method of investigation. In this field the work of Harrison (3) is particularly noteworthy. He removed portions of the neural wall of frog embryos and mounting them in frog lymph was able to observe the outgrowth of the axones of the living neuroblasts and to measure the rapidity and extent of growth. The enlarged end of the growing axone presented projections which were being protruded and withdrawn, giving an appearance similar to that represented by Held and others as seen in microscopical sections of embryos. Harrison interpreted this appearance as indicating that the outgrowth of the axone is really a form of amoeboid motion.

Further, Burrows (2) adapting Harrison's technique to the chick embryo and mounting portions of the neural wall in hen lymph, was able to watch the outgrowth of the axone and to measure its rate and extent. Also, he proved by using neurofibril stains that this outgrowth is accompanied by a differentiation of the neurofibrils, presenting appearances similar to those represented by Held in his diagrams of sections of the developing nervous system of the chick.

These observations prove beyond doubt that the axones of neuroblasts of frog and chick embryos when placed in suitable media are outgrowths from the cell body as the formative center, and as this outgrowth is accompanied by appearances already observed in sections and by the normal process of neurofibrillar differentiation, it can not be considered an abnormal phenomenon due to an unusual environment, but represents essentially what occurs in the bodies of the embryos. They disprove Held's statements that amoeboid movement of neuroblasts does not occur and that axones can only grow out under the influence of the plasmodesms.

In summation, we may say that the weight of evidence from histology, physiology and pathology at the present time is very strongly in favor of the neurone theory, and that the evidence from experimental embryology seems conclusive that the nerve cell is a genetic unit with its formative center in the nuclear and perinuclear regions, and this we consider the essential criterion of the neurone theory.

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THE PHYSIOLOGY OF NERVE

BY EDWIN B. HOLT

Harvard University

A valuable survey of the neuro-fibrillar theory,¹ and of observations antagonistic to the discontinuous neurone theory, has been made by Frankfurter (2) who is a partisan of the former view. "The fibrillæ are not interrupted from the spot where they take up the sensory stimulus, to their point of motor discharge"; indeed they appear to grow directly into the muscle fibers. Frankfurter admits no 'synaptic membrane' and describes the course of a fibrilla from axis-cylinder to cell-body and on to axis-cylinder, as follows:—axis-cylinder, inner network close around the nucleus of the cell-body, outer perinuclear network (surrounding the inner), dendrite, interneuronal or 'diffuse' (Apáthy) network, terminal arborization, axis-cylinder (of the next neurone). "It follows directly that all those fantastic notions, put forward specially by French authors, but also for instance by Cajal, of sleep, association, etc., as being due to active or passive movements of the dendrites—are utterly erroneous." Nor are any new connections made or paths formed in the individual's life, they merely are made 'gangbar'—'ein physiologisch leichter verständlicher Vorgang der Bahnung.' There are no 'specifically' different nerve activities, either in fibril or ganglion; nor any brain localization in the old sense. F. admits that the complete fibrillar

¹ See preceding article.

continuity and the *nervous* nature of the extracellular (diffuse) network, are still matters of dispute. v. Lenhossék (10) contends that the neuro-fibrils are not the specifically conducting elements of the nervous system; their significance is histo-genetic.

After the work on the periodic quality of the nervous impulse, stimulated mainly by H. Piper and by the advent in physiology of the string galvanometer, the most important advance in nerve physiology is, doubtless, Nernst's theory of electrical stimulation. This supposes the electrical excitation to produce its effect by concentrating the ions by which it is carried, at membranes (impermeable to the ions) which are contained within the excitable cell. Nernst's formula has in general held its own; but it fails to account for the inefficacy of slowly increasing, and of high-frequency, currents to excite nerve and other tissue. Hill (5) now develops Nernst's thought, and deduces a more adequate formula which Lucas, in an extremely well-written paper (11), shows to fit several observed facts which Nernst's own equation does not fit. This is an extension rather than a refutation, of Nernst's thought. "The characteristic time-factor in excitation is determined . . . by the rate of diffusion of the ions concerned. The factors which condition this rate are the diffusion constant of the ion concerned, and the distance between the membranes." v. Zeynek and v. Bernd (17) consider the bearing on Nernst's theory of the fact that electric oscillations of the high frequency used in wireless telegraphy do not stimulate tissues: and in general they confirm the theory. Hoorweg (7) agrees with Hill and Lucas in the inadequacy of Nernst's original 'square-root law.' Weiss (16) offers a (certainly too) simple formula which would if adopted displace that of Nernst.

Dittler (1), working with Einthoven's galvanometer, finds it probable that "the voluntary tonic muscle contraction should be considered as a muscle tetanus [cf. H. Piper], in which the action current of the muscle closely reproduces the discontinuous stimuli coming to it from the nerve. It is still an open question whether the activity of the central organ is itself discontinuous, and whether its periods coincide with those of the nerve and muscle." Höber (6) has tried to discover, by using the ultra-violet microscope, visible changes in the colloidal substance of axones as these were traversed by nervous impulses. The experiment has been so far unsuccessful. Oinuma (13) reports that for the single nerve fibril there is no sub-maximal mechanical stimulus, *i. e.*, if a mechanical interference stimulates the single fiber at all, it stimulates maximally.

The 'Treppe' and allied phenomena have attracted considerable experimental attention. Gotch (4) studies in the excised sciatic nerve of the frog a phenomenon previously described by Lucas in connection with the electrical response of the sartorius muscle;—this is "a modification in the time of commencement of the second response when evoked by a stimulus occurring at certain intervals after its predecessor; this time . . . may be greatly delayed and the second response appears to commence after this prolonged delay at the same moment even when the actual moment of stimulation is shifted through a considerable range of time." Thus in the sartorius muscle the true refractory period is succeeded by one in which the tissue can receive and hold a stimulation but cannot develop or propagate it. Gotch finds this same phenomenon in excised sciatic nerve. "The range of time within which the second stimulus can evoke a response with this extra delay is about 5/1000 sec. for temperatures from 3° to 8°; at 12° C. the range is much shortened." It is not true of nerve at the higher temperatures (as it is of m. sartorius) that the second response commences at the same delayed moment even though the second stimulus is varied as regards its moment of application. "There is, in nerves at 12° C., distinct evidence of true nerve fatigue, showing itself only as retarded propagation." It is "present in all parts of the nerve which have been previously traversed by a sufficient succession of nerve impulses." In muscle this second response, although delayed, is generally greater than the first (Treppe), a phenomenon ordinarily attributed to facilitation (Bahnung): but owing to the conjoined delay some authors favor the phrase 'apparent facilitation' (scheinbare Bahnung). Ishikawa (8) discusses this matter. Lucas (12) finds that the delay of the second response is "due entirely to a modification of the tissue by the previous propagated disturbance," and not to any "direct local action of the previous stimulating current." Tait (14) discusses the relations between 'absolute' and 'relative' refractory phases on the one hand and the electrical 'wave' accompanying activity on the other. Tiedemann (15) discusses absolute refractory phase in a somewhat comparable manner.

A paper by Göthlin (3) must find mention even in the brief space remaining. Göthlin argues, on experimental grounds, that reinforcement of the nervous impulse takes place along the path of conduction itself (axone); that the insulation of the nerve, the myeline, is not a perfect insulator; that the electrical resistance of the axis-cylinder is very great, "and can in a moderately large (4.34 μ) nerve

fiber of the corpus callosum [cow] amount to no less than 20,000,000 ohms per centimeter"; and, lastly, that the relatively low speed of nerve conduction affords no ground for denying the electrical nature of the nervous impulse.

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THE GALVANIC PHENOMENA

BY KNIGHT DUNLAP

The Johns Hopkins University

There has been a considerable addition, during 1909 and 1910, to the literature concerned with electric currents obtainable from animal tissues under various conditions. The action-currents of muscles, and the so-called skin-currents have been given much attention, and the phenomena connected with the electrocardiogram have been investigated by a large number of physiologists and medical men, chiefly from the diagnostic standpoint. It is quite unnecessary and impossible to review this literature here, although it is of prime importance in connection with the study of the so-called psycho-galvanic phenomena. Barker (1) has given a most excellent historical and technical account of the electrocardiogram work, with abundant references, and this is undoubtedly the best introduction to the subject which has yet appeared. The increasing interest in electrophysiology is well illustrated by the space allotted to the topic in the new editions of two standard text books. The chapter in Stewart (16) is very full, and the chapter in Howell (5) is nearly as adequate.

The technique of the string-galvanometer, the instrument now accepted as standard for electro-physiological research, has been given due attention. Einthoven (3) has published a full account of the latest model of the instrument, and Westerlundt (19) has made a careful study of the rise in temperature and consequent decrease in sensitivity of the instrument under working conditions, attributing the lowering of the sensitivity to increased tension on the string.

Grau (4) gives new data on the influence on the cardiogram form exercised by the position of the heart, and by inspiration and expiration, and Straub (17) details the finding of a change in the galvanometric deflection produced by the intravenous injection of agents (strophantin and adrenalin) producing vaso-constriction, when the current was led off from asymmetrical locations, the effect being independent of the heart-action; but neither these nor any others of the large number of experimenters on the electrocardiogram make any attempt to bring the phenomena into relation with the so-called psycho-galvanic reaction.

Piper (10) has repeated in a more careful way his former work on the velocity of the nervous impulse, recording by the string galvanometer both the muscular action-current and the stimulus to the nerve. The rate is found to be 123 m. per sec., and to be independent

of the intensity of the excitation. Snyder (14), applying Piper's method to the measurement of the latency of the knee-jerk response, has concluded that the reflex is neural. These investigations doubtless foreshadow a wider application of electro-physiological methods to neurological problems.

The research which is of most importance for the psycho-galvanic work, is probably that of Orbeli (7), on skin-currents. Orbeli discarded the old method—the application of electrodes directly to the outer and inner surfaces of the skin—using instead salt solutions for both sides (with non-polarizing electrodes leading from the solution), or salt solution applied to outer skin (frog's leg in jar) and non-polarizing electrode bound to a surface from which the skin was removed. The use of water, or NaCl solution not over .003-.005 per cent., on the outer surface gave usually a weak current of rest directed *outwardly*; sometimes the current was directed *inwardly*, but was always weak. Stimulation of the nerve supplying the area gave in every case a response current directed *inwardly*. When NaCl or KCl solution stronger than .003-.005 per cent. was used on the outer surface, the current of rest was always directed *inwardly*, and was relatively strong. Stimulation of the nerve gave always an *outwardly* directed response current. It made no difference what solution was used on the inner skin surface. These results would seem to the reviewer to suggest strongly that the chemical action of electrolyte and skin secretions plays a large part in the production of skin-currents and in other electrical phenomena where current is led off from the skin.

In the specific field of the psycho-galvanic reflex, no great progress has been made, and the summary of Piéron (9) seems to hold true: "il n'y a là qu'une méthode d'appoint particulièrement délicate dans la pratique, extrêmement dangereuse dans l'interprétation, et difficilement utilisable la plupart du temps en médecine mentale."

Veraguth (18) is strongly convinced that the current-variations are due to true action-currents from the sweat-glands, the action of belladonna in decreasing the effect seeming to speak strongly for this conclusion. Müller (6), who used battery and fluid electrodes, thinks that the effect is due to polarization, pointing out that the characteristic rest- and response-deviations are obtainable only from the palms and soles, although sweat-glands are found in other regions. The rest-current, in Müller's experiments, showed a decided drop-curve, the decrease in the deflection (d'Arsonval) being as much as 40 per cent. in six seconds. This curve could be repeated indefinitely by simply removing the hands from the solutions and replacing

them. Müller also found that the amount of skin surface immersed made a great difference in the deflection, but that the use of needle electrodes concurrently with the fluid made practically no difference, although the needle electrodes alone conducted current fairly well.

Sidis and Kalmus (12), working with the d'Arsonval galvanometer, and battery, in series with copper electrodes in concentrated NaCl solution, found that "pure ideational experiences" gave no change in the deflection, while "sudden violent emotions, and especially intense stimulation of a painful or of a disagreeable nature," produced an increase in the deflection. They found also that "muscular activity of those parts of the body actually forming the circuit bring about galvanometric deflections, while activity of the more remote parts of the body are ineffective." Curiously enough, however, "violent stirring of the liquid with the hands did not change the reading of the galvanometer."

Starch (15), working with battery and mercury-calomel-saline electrodes, found that mental processes produced a slight increase in the deflection and that emotional processes and muscular activity produced larger deflections. Apparently this is satisfactory evidence that a motor discharge is a necessary antecedent to the galvanic phenomena.

Sidis and Kalmus worked also without battery, using electrodes of unspecified type applied to the hands or hand and mouth, and found decided 'deflections.' Apparently this work was done with the capillary electrometer, as they say: "We repeated Waller's experiment, but could not confirm his results." It seems that they used much stronger solutions than did Müller, which probably accounts for the difference in results. They say: "Different experiments performed with different concentrations of electrode solutions gave different deflections, in fact, the direction and magnitude was varied at will in this way." "Different parts of the skin gave different steady deflections. However, superimposed upon this original steady deflection is a deflection due to the various stimulations given." In strong contrast with these results are the results stated by Sidis (11) in connection with experiments with metal electrodes: "We inserted platinum needle-electrodes in different parts of the body, in the same limb, or in different limbs, or but a few inches apart, and found no deflections whatever. . . . There is no current of rest." "The place of insertion of the electrodes makes no difference whatever in the galvanometric deflections." That the deflections obtained by Sidis and Kalmus depended rather directly on the action

of electrolytes on the skin secretions, is evidenced by the fact that, according to their statements, reversing the positions of the hands in the electrode solutions did not in most cases reverse the galvanometric deflections; although this may not be significant, if the experimenters were actually using the capillary electrometer and not the d'Arsonval galvanometer.

The experimenters attempted to limit the action of the skin by coating with shellac and paraffin the whole of the hand with the exception of the nails, which were left exposed. Under these conditions the characteristic deflections were obtained. Peterson and Scripture (8), however, are of the opinion that the insulation was imperfect, since they found that coating the skin with paraffin or shellac cut out the current completely. It must be noted that Müller found that coating the whole hand with a layer of lanolin and vaseline 2 mm. thick did not completely cut out the current.

Sidis and Nelson (13) worked with the d'Arsonval galvanometer without battery, with platinum electrodes inserted in the tissues of rabbits and frogs. According to their account and curves, they obtained in most cases initial deflections which in a short time returned to zero, and were renewed by muscular activity. I have pointed out in another place (2) the probability that this is a polarization effect, or at least an effect produced by action of the bodily fluids on the platinum.

The psycho-galvanic phenomenon has not yet been given a satisfactory interpretation, but several significant points have been brought out. The importance of the nature and concentration of the electrolytes, the effects of the motor discharge to the region from which the current is taken, or regions through which the current flows, and the influence of drugs acting on the glandular and vascular systems, have been brought out in a way which indicates the line of future research.

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NOTES AND NEWS

The Fourth International Congress of Philosophy was held at Bologna April 6-11. One of the eight sections was devoted to psychology. On the preliminary circular there were announced for this section sixteen titles covering a wide range of psychological topics.

Nature announces that plans are well under way for the erection at Cambridge of a building for the projected psychological laboratory.

Professor G. M. Whipple, of Cornell University, will give two courses at the coming summer session of Columbia University. The subjects of the courses will be, respectively, Mental Development, and Psychological and Educational Measurements. Professor Kirkpatrick, of the Fitchburg Normal School, will replace Professor Whipple at the Cornell summer school and offer courses in educational psychology.

The third annual meeting of the Minnesota Psychological Conference was held at the University of Minnesota March 31, 1911. The program was devoted chiefly to the educational applications of psychology.

The present number of the BULLETIN, dealing especially with nerve physiology, has been prepared under the editorial care of Roswell P. Angier.

